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Fire and windthrow in forests: Winners and losers in Neuropterida and Mecoptera

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Abstract

The mid-term impact of forest fires and windthrows on species compositions in the insect orders Neuroptera, Raphidioptera, and Mecoptera was assessed in Swiss forests using standardized flight interception traps. For 50 species the abundances in intact control plots were compared to those in moderately or strongly disturbed forest stands. The catches were combined over four forest disturbance projects, ranging from windthrows in alpine spruce forests and lowland deciduous forests to winter forest fires in Southern Switzerland and a large summer fire in southwestern Switzerland. As a result, 82% of the 50 species benefited from the disturbance and became more abundant in the years after the fire or windthrow. More species (19) had their maximum abundance in intermediately disturbed plots than in heavily disturbed forests (17). Only 11 species, mainly Hemerobiidae and Coniopterygidae, peaked in the undisturbed forest stands. The species are listed per impact and ranked as winners (more than 66% specimens per treatment collected in disturbed forest plots), losers (more than 66% specimens per treatment in undisturbed forest plots), and indifferent species. An additional 29 species that were too scarce for an assessment are listed in Appendix 1. We conclude that for Neuropterida and Mecoptera catastrophic incidences are natural ecological events which create new habitats and by this foster their occurrence and abundance.

Introduction

Natural disturbances such as strong storms causing windthrow in forests or wildfires destroying the vegetation have a drastic impact on the survival of plants and animals (Schelhaas et al. 2003). While a catastrophe for forestry, such stochastic or recurring disturbances are natural phenomena that have led to well-adapted communities of plants and animals. After Bond and Keeley (2005), fire in natural ecosystems is a significant evolutionary force. Research after forest fires and windthrows have shown that many species are benefiting from natural disturbances (Wermelinger et al. 1995, 2002, 2017, Moretti et al. 2002, 2006, 2010, Bouget and Duelli 2004), or even depend on them for their long-term survival (e.g. Ressl 1969, Bond and Keeley 2005).

Apart from earlier more general assessments of Neuropterida survival in three of the four projects presented here (Duelli et al. 2002a, Moretti et al. 2006, 2010, Wermelinger et al. 2017), we were not able to find published information on natural disturbances such as forest fire or windthrow affecting populations of Neuropterida or Mecoptera. While a broad range of arthropod orders and families have been sampled in the projects described here, the present paper is limited to the insect orders Neuroptera, Raphidioptera, and Mecoptera (Megaloptera were absent). These small orders (Aspöck et al. 1980, Willmann 1989) are very ancient clades. The species are mainly predaceous both as adults and larvae and preferentially feed on soft-bodied arthropods. The aim here is to present a detailed assessment of natural disturbances on populations of abundant species of Neuroptera, Raphidioptera, and Mecoptera.

Material and methods

Collecting method

Two similar types of trap stations were used for sampling Neuroptera, Raphidioptera, and Mecoptera. In the windthrow project in Alpine spruce forests each trap station consisted of a window trap and a yellow bucket trap (Fig. 1). The window trap intercepted flying insects with a vertical glass screen (80 cm × 50 cm) mounted 150 cm above ground with two lateral water troughs 80 cm long (Duelli et al. 1999). Some detergent was added to the water to make the insects drown quickly, and 2% Rocima GT (Acima, Buchs, Switzerland) was also added to prevent mold. The yellow bucket traps, 20 cm in diameter, attracted flower-visiting insects. They were also filled with water containing some traces of detergent and Rocima. For the three other projects a newer type of combined trap (further as combi-trap, Fig. 2) was used (Duelli et al. 1999). The combi-traps consisted of two sheets of Plexiglas (50 cm × 43 cm) crossed at right angles to provide independence of wind direction. To collect the insects, a yellow plastic funnel (43 cm diameter) was mounted below the screens, again at a height of 150 cm and filled with water and the same additives as above. A comparison between the performance of one window trap plus one yellow bucket vs. one combi-trap showed no statistically significant differences in species composition, richness and abundance (Gygax 1999).

Trap numbers and sampling periods varied between projects, but were always identical among the three treatments within one project (see below). The traps were emptied weekly. The sampled material was stored in vials with 70% EtOH and sorted to taxonomic groups. The specimens of Neuropterida and Mecoptera were identified by the first author using the nomenclature of the lacewing digital library (Oswald 2017) and for Mecoptera Klausnitzer (2002).

Experimental design

Two projects investigated the impact of windthrow on the insect fauna: in the Northern Pre-Alps (Windthrow I), and on the Swiss Plateau (Windthrow II). Two other projects analyzed the impact of forest fire: one encompassed multiple fire on the southern slope of the Alps in Ticino (Forest Fire I), the other was a large wildfire in the inner-Alpine valley Valais (Forest Fire II). Table 1 shows the location of the different projects and trap sites.

Each of the four projects included three different treatments. Intact, undisturbed forests (FO) served as controls, heavily disturbed (HD) plots were plots with maximum disturbance, and intermediately disturbed (ID) plots were less severely disturbed. More detailed descriptions of the treatments are given below.

Windthrow I (Vivian)

In early 1990 storm Vivian devastated mainly subalpine spruce forests in the Swiss Alps (Fig. 3). Near the village Schwanden at elevations around 1000 m three forest

Figure 1. Window interception trap and yellow bucket trap in an uncleared windthrow plot (Windthrow I) above Schwanden after storm Vivian. Photo: WSL.

Figure 2. Combi trap (a combination of a flight interception trap and a yellow funnel trap) in an uncleared windthrow plot (Windthrow II) near Habsburg after storm Lothar. Photo: WSL.

Table 1. Trap location and site numbers of the four projects.

Project	Canton	Community	Locality	Treatment	Latitude	Longitude	m above sea	N sites
Forest Fire I	TI	Brissago	Boscopiano	control	46.133936	8.712697	560	3
			Ciossa	control	46.105821	8.692639	460	3
		Gordola	Falò	control	46.191353	8.840348	590	3
			Monti di Ditto	control	46.184869	8.890699	730	3
		Locarno	Canegg	control	46.175529	8.772595	460	3
		Minusio	Ronco di Bosco	control	46.184160	8.803246	660	3
		Gordola	Sassone	repeated fires	46.192194	8.863041	845	6
		Locarno	Ai Sassi	repeated fires	46.176832	8.776513	575	6
			Monte Bré	repeated fires	46.181748	8.779224	890	3
		Ronco sopra Ascona	Buffaga	repeated fires	46.142842	8.720671	520	3
		Brissago	Sciresa	single fires	46.113481	8.691522	680	3
		Gordola	Selvacce	single fires	46.195802	8.844349	580	3
		Locarno	Piodelle	single fires	46.183951	8.783164	920	3
		Minusio	Ronco di Bosco	single fires	46.185028	8.805859	670	3
		Orselina	Gaggio	single fires	46.182509	8.790900	660	3
		Ronco sopra Ascona	Fontana Martina	single fires	46.138382	8.717330	480	3
Forest Fire II	VS	Leuk	Höhwald	Forest Fire Edge	46.329863	7.649166	1427	6
				Forest Fire Center	46.330463	7.650454	1433	6
				Forest	46.330736	7.650295	1442	6
Windthrow I	GL	Schwanden (GL)	Schwanden, GL (Niederntal)	Uncleared	46.980930	9.094159	1000	5
				Cleared	46.983742	9.095598	1000	5
				Forest	46.981916	9.090925	1000	5
Windthrow II	AG	Habsburg	Habsburg	Uncleared	47.469381	8.204498	420	3
				Cleared	47.457359	8.196624	430	3
		Brugg	Habsburg	Forest	47.495900	8.203981	440	3
	SO	Messen	Messen	Uncleared	47.086577	7.464313	535	3
				Cleared	47.088782	7.461421	530	3
				Forest	47.084293	7.459738	545	3
	AG	Sarmenstorf	Sarmenstorf	Uncleared	47.318269	8.257562	580	3
				Cleared	47.318752	8.255356	590	3
				Forest	47.281080	8.288693	715	3

Figure 3. Large windthrow of storm Vivian in spruce forest in the Canton Glarus. Photo: WSL.

Figure 4. Cleared windthrow plot above Schwanden three years after storm Vivian (Windthrow I). Photo: WSL.

plots were used for a long-term investigation of different disturbance effects on biodiversity between cleared and uncleared windthrows. Like the disturbed plots, the control forest plot (FO) consisted of intact spruce forest with some scattered deciduous trees. The HD and ID plots had been equally affected by the storm but HD was cleared of all stems, suffering a double disturbance: windthrow and timber harvest (Fig. 4). In the ID plot the fallen trees remained untouched by harvest (Fig. 1). In the disturbed plots of 1–2 ha the vegetation cover developed slowly because of the high elevation. While in the cleared plot (HD) flowering herbs attracted pollinators and pollen feeders, the uncleared plot (ID) developed a brush vegetation of deciduous plants and young trees. The plots were sampled in 1992 (two years after the storm), 1993, 1994, 1996, 2000 and 2009. Three window traps and five yellow bucket traps were placed in each of the three plots (FO, ID, HD) at distances of at least 30 m between trap stations. The sampling periods lasted from mid May to end of September.

Windthrow II (Lothar)

Ten years after storm Vivian, storm Lothar (late 1999) devastated even larger forest areas all over Europe. This time mainly deciduous forests in the Swiss Central Plateau were affected. Three areas, each with the three types of treatments (intact forest FO, cleared HD, and unsalvaged ID) were secured for long-term investigation. The plots in the region of Sarmenstorf (Fig. 2) represented beech forest (*Fagus sylvatica* L.), those at Messen were spruce forests (*Picea abies* (L.)), and those at Habsburg were mixed forest with half coniferous (mainly spruce) and half broad-leaved trees (Fig. 5). Within a region, the three treatments were located at distances from 100 m to three km apart to keep site conditions similar. In each of the nine plots three combi-traps were placed at distances of about 100 m from each other. A total of 27 combi-traps were operated between mid March to end of September in the years 2001, 2004, and 2010.

Forest fire I (Ticino)

The study area stretched over 15 km along a south-facing slope of the Swiss Alps at elevations between 450 m and 850 m a.s.l. in the region of Locarno. The former coppice stands of chestnut forest (*Castanea sativa* L.) on acidic soil is prone to forest fire, mainly fast spreading surface fires in late winter. Detailed records of the incidence of fires in that region (Conedera et al. 1996) allowed for a sampling design based on "space for time substitution" (Pickett 1989). Instead of sampling in different years after a fire, plots with different fire histories were sampled within one year (Moretti et al. 2006). In six sectors, 18 trap sites were chosen, each with a plot of only one fire for the previous 40 years (intermediately disturbed; ID), another with two to four fires in the previous 40 years (heavily disturbed; HD), and the third with no fire in at least 40 years (undisturbed

Figure 5. Cleared windthrow plot in mixed forest near Messen, two years after storm Lothar (Windthrow II). Photo: WSL.

forest; FO). All plots had similar site conditions. The same combi-traps (Fig. 6) as in windthrow project II (Lothar) were used (Moretti et al. 2006). Three traps were placed in each of the 54 plots. The minimum distance between traps at each site was ten m, while the average distance between the sites was around 300 m. The traps were emptied weekly from March to September 1997.

Forest fire II (Leuk)

On 13 August 2003, 300 ha of south-exposed forest at Leuk in the dry Central Alpine valley of the Valais fell victim to a large forest fire caused by intentional arson (Wohlgemuth et al. 2005). The burned area consisted of different forest types at elevations from 800m to 2100 m a.s.l. Three horizontal transects of six combi-traps were installed at elevations of 1200 m (mainly *Pinus sylvestris* L.), 1450 m (mixed forest with *Picea abies* and *Pinus sylvestris*), and 1700 m (mixed forest with *Larix decidua* Miller and *Picea abies*), ranging on both sides of the burned area from intact forest (FO) into the center of the burned area (HD, Fig. 7). The traps in the intermediately disturbed areas (ID) were installed on burned ground, but close (20–50 m) to the remaining forest edges. The 18 combi-traps (six at three altitudes) were emptied weekly from April to early September, starting in 2004 (first year after the fire) and continuing in 2005, 2006, 2008, and 2013. Details on regrowth of the vegetation at different locations and altitudes (Fig. 8) are given in Moser and Wohlgemuth (2006).

Data processing

Natural impacts such as wildfires or windthrows cannot be planned or organized in space and time, because they happen sporadically and accidentally. Scientific investigations are therefore case studies rather than experiments with true replicates for statistical treatment. Replicates of either windthrow or forest fires take place in different years, show different coverage, or even occupy different regions. Since the projects were located at different elevations and in different regions of Switzerland, several species occurred only in a subsample of the projects. This heterogeneity prevented us from averaging numbers of specimens per treatment and from calculating variance. Also, the abundance of species changed with time after the impact, which cannot be considered as a variable in the present analysis because of the low numbers of specimens collected for most species. Furthermore, spatial autocorrelation of the trap sites (or plots) is a critical issue in unique events, but in the case of repeated space for time substitution (fire in Ticino) we accounted for it and minimized its effect by avoiding spatially structured sampling design (Moretti et al. 2010).

For each of the four projects, species lists were established. For each species the numbers of specimens collected per treatment (FO, ID, HD) were combined for all years. A species had to be caught at least five times in all four projects to be included in the analyses. Species collected in smaller numbers are listed in Appendix 1 for faunistic considerations only.

Figure 6. Combi trap in an intensely disturbed forest plot in Ticino (Forest fire I) after several forest fires within the previous 40 years. In spring the chestnut regrowth (here without old trees) is still without leaves. Photo: WSL.

Figure 7. Combi trap in the center of the large burned area above Leuk, a few months after the fire (Forest fire II). Photo: WSL.

Figure 8. Two years after the massive fire above Leuk the whole area was covered with a carpet of colorful vegetation. Photo: WSL.

To quantify the positive or negative impact of disturbance on a species, the numbers were combined separately for the three treatments FO, ID, and HD for all four projects. The number of trap sites per treatment was balanced. As an indicator for the effect of disturbance in general, the following formula was used for each species: mean (HD+ID) / (mean (HD+ID) +FO). Species with more than 66% are considered winners, those with less than 33% losers.

Species rating in between are considered indifferent to the midterm effects of storms or fires.

Results

In total, 8345 individuals from 79 species were collected. Among the 8285 specimens of the 50 more common species, the most species-rich order was the Neuroptera, numbering 42 species, whereas the most abundant order was the Mecoptera where only five species included a total of 4291 specimens (Table 2). Raphidioptera numbered only three species, but were represented by a total of 1037 individuals. The most species-rich projects were the forest fire projects in Leuk (56 species) and in Ticino (37 species). Only nine species were collected in all four projects, six were found only in Leuk, and two only in Ticino. Among the 29 scarcely collected species (Appendix 1), 16 belong to the Hemerobiidae, five to Chrysopidae, four to Coniopterygidae, two to Raphidioptera, and one each to Myrmeleontidae and Osmylidae.

A majority of 20 species were most abundant in the intermediately disturbed plots (ID) (bold print in Table 2). Fewer species (17) were most abundant in the highly disturbed (HD) plots, and only 11 species in the undisturbed (FO) forest sites. Two species were equally abundant with their maxima in the two disturbed plots (ID and HD). In the Vivian windthrow project the HD plots yielded the highest species numbers, while in the Lothar windthrow project the two disturbance treatments yielded equal numbers. In the forest fire project above Leuk the highest number of species was captured in the ID plots, and in Ticino all three treatments yielded about the same number of species. Of the total of 8285 individuals, 42% were caught in the ID plots, 37% in the HD plots, and 21% in the FO plots.

For each species the sum (N) of all specimens collected per treatment (FO, ID, HD) is shown in Table 2 for each of the four projects. Not all species were consistent

Table 2a. List of species of families Chrysopidae and Hemerobiidae with five or more specimens collected in the three treatments (FO: intact forest; ID: intermediately disturbed plots; HD: heavily disturbed plots) of the four projects. The grand total gives the sum for all projects. The treatment with the highest number of individuals is highlighted in bold. Two equally high numbers are also highlighted. Single specimens in one or two treatments are not highlighted. Calculation of % in disturbed plots: mean(HD+ID)/(mean(HD+ID)+FO). Values for the Grand Total are considered. Species above 66% are considered winners, those below 33% losers.

Order	Family	Species	% in disturbed plots	Winners / Losers	All Disturbances				Forest Fire								Windthrow							
					Grand Total				I. Ticino				II. Leuk				I. Vivian				II. Lothar			
					N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD
Neuroptera	Chrysopidae	*Chrysopa formosa* Brauer	100%	W	25		**17**	8					25		**17**	8								
		Chrysopa pallens Rambur	100%	W	7		2	**5**					7		2	**5**								
		Nineta flava (Scopoli)	100%	W	5		**5**						5		**5**									
		Pseudomallada prasinus (Burmeister)	100%	W	145		**76**	69	1			1	144		**76**	68								
		Pseudomallada ventralis (Curtis)	100%	W	24		**16**	8					20		**14**	6	3		**2**	1	1			1
		Chrysopa perla (L.)	97%	W	229	4	101	**124**	5		2	**3**	130	3	52	**75**	74	1	**38**	35	20		9	**11**
		Chrysoperla lucasina (Lacroix)	96%	W	267	6	124	**137**	3		1	**2**	215	3	**109**	103	8			**8**	41	3	14	**24**
		Pseudomallada abdominalis (Brauer)	85%	W	12	1	3	**8**					4		1	**3**	4	1		**3**	4		**2**	**2**
		Pseudomallada flavifrons (Brauer)	83%	W	53	5	**38**	10	5		**4**	1	43	5	**32**	6					5		2	**3**
		Cunctochrysa albolineata (Killington)	78%	W	8	1	**4**	3					4		**2**	**2**	4	1	**2**	1				
		Chrysoperla carnea (Stephens)	65%	–	537	113	196	**228**	204	69	65	**70**	110		**66**	44	2			**2**	221	44	65	**112**
		Hypochrysa elegans (Burmeister)	58%	–	26	7	**10**	9	2	1	1										24	6	**9**	**9**
		Nothochrysa fulviceps (Stephens)	43%	–	5	**2**	1	**2**					2		1	1	1	1			2	1		1
		Chrysoperla pallida Henry, Brooks, Duelli & Johnson	40%	–	139	**59**	39	41	22	**13**	5	4	16	2	**7**	**7**					101	**44**	27	30
		Chrysotropia ciliata (Wesmael)	23%	L	86	**54**	16	16	1	1											85	**53**	16	16
		Peyerimhoffina gracilis (Schneider)	13%	L	13	**10**	1	2					5	**5**			1	1			7	**4**	1	2
		N individuals			1581	262	649	670	243	84	78	81	730	18	384	328	97	5	42	50	511	155	145	211
		N species; with ≥ 5 inds.			16	11	16	15	8	4	6	6	14	5	13	12	8	5	3	6	11	7	9	11
	Hemerobiidae	*Megalomus tortricoides* Rambur	100%	W	5		2	**3**					2			**2**	3		**2**	1				
		Wesmaelius subnebulosus (Stephens)	83%	W	142	13	41	**88**	25	3	5	**17**	115	10	36	**69**	1			1	1			1
		Wesmaelius malladai (Navas)	81%	W	85	9	34	**42**					85	9	34	**42**								
		Micromus paganus (L.)	81%	W	47	5	16	**26**	1	1			11	3	7	1	35	1	9	**25**				
		Megalomus hirtus (L.)	80%	W	9	1	4	**4**					5		2	**3**	4	1	2	1				
		Micromus angulatus (Stephens)	80%	W	9	1	5	3	2	1		1	2		1	1					5		4	1
		Micromus variegatus (Fabricius)	78%	W	73	9	**29**	**35**	39	6	11	**22**	21	2	**10**	9	3		2	1	10	1	6	3
		Hemerobius lutescens Fabricius	74%	W	40	6	15	**19**	8	**4**	3	1	28	2	12	**14**	4			**4**				
		Hemerobius humulinus L.	70%	W	124	22	28	**74**	98	18	16	**64**	11	1	4	**6**	8	**3**	3	2	7		**5**	2
		Drepanepteryx phalaenoides (L.)	70%	W	10	3		**7**	9	2		**7**					1	1						
		Hemerobius micans Olivier	48%	–	235	82	**100**	53	159	53	**62**	44	4	1	**3**		38	**20**	17	1	34	8	**18**	8
		Sympherobius klapaleki Zeleny	18%	L	23	**16**	6	1	22	**15**	6	1									1	1		
		Hemerobius pini Stephens	13%	L	16	**14**	2						10	**9**	1		4	**4**			2	1	1	
		Sympherobius fuscescens (Wallengren)	13%	L	8	**7**		1					4	**3**		1	2	**2**			2	**2**		
		Sympherobius pellucidus (Walker)	0%	L	12	**12**							8	**8**			3	**3**			1	1		
		N individuals			838	200	282	356	363	103	103	157	306	48	110	148	106	35	35	36	63	14	34	15
		N species; with ≥ 5 inds.			15	14	12	13	9	9	6	8	13	10	10	10	12	8	6	8	9	6	5	5

regarding their total maxima. The most consistent group of species was that of the intact forest dwellers (maximum of specimens in FO). Four species were consistent only because they were restricted to one project.

The impact strength of disturbance is expressed as the percentage of population gain or loss after the fire or windthrow (left column in Table 2). With no specimens caught in the intact forest plots, the positive impact on a species

Table 2b. List of species of Coniopterygidae, Myrmeleontidae, Raphidiidae, and Panorpidae. Further explanations as in Table 2a.

Order	Family	Species	% in disturbed plots	Winners / Losers	All Disturbances				Forest Fire								Windthrow							
					Grand Total				i. Ticino				ii. Leuk				i. Vivian				ii. Lothar			
					N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD	N	FO	ID	HD
Neuroptera	Coniopterygidae	*Coniopteryx esbenpeterseni* Tjeder	91%	W	22	1	10	**11**	12	1	2	**9**					10		**8**	2				
		Parasemidalis fuscipennis (Reuter)	90%	W	20	1	**16**	3	2		**2**		1	1			17		**14**	3				
		Coniopteryx borealis Tjeder	67%	W	5	1	**3**	1	4	1	**2**	1					1		1					
		Coniopteryx tineiformis Curtis	57%	–	66	18	**30**	18	54	17	**21**	16					11	1	**8**	2	1		1	
		Coniopteryx haematica McLachlan	50%	–	6	2	**3**	1	6	2	**3**	1												
		Coniopteryx drammonti Rousset	33%	–	10	**5**	4	1	10	**5**	4	1												
		Semidalis aleyrodiformis (Stephens)	31%	L	305	**161**	105	39	304	**160**	105	39	1	1										
		Coniopteryx pygmaea Enderlein	24%	L	54	**33**	10	11	12	4	**5**	3	33	**23**	5	5	8	**6**		2	1			1
		Conwentzia psociformis (Curtis)	0%	L	6	**6**			3	**3**			3	**3**										
		N individuals			494	228	181	85	407	193	144	70	38	28	5	5	47	7	31	9	2	0	1	1
		N species; with ≥ 5 inds.			9	9	8	8	9	8	8	7	4	4	1	1	5	2	4	4	2	0	1	1
	Myrmeleontidae	*Distoleon tetragrammicus* (Fabricius)	94%	W	32	1	**19**	12					32	1	**19**	12								
		Myrmeleon formicarius L.	75%	W	12	3	**9**						12	3	**9**									
		N individuals			44	4	28	12					44	4	28	12								
		N species; with ≥ 5 inds.			2	2	2	1					2	2	2	1								
Raphidioptera	Raphidiidae	*Phaeostigma notata* (Fabricius)	91%	W	311	14	**164**	133					242	7	**130**	105	40	6	11	**23**	29	1	**23**	5
		Dichrostigma flavipes (Stein)	88%	W	710	46	**419**	245					710	46	**419**	245								
		Puncha ratzeburgi (Brauer)	60%	–	16	4	**6**	**6**					6	**3**	2	1	10	1	4	**5**				
		N individuals			1037	64	589	384					958	56	551	351	50	7	15	28	29	1	23	5
		N species; with ≥ 5 inds.			3	3	3	3					3	3	3	3	2	2	2	2	1	1	1	1
Mecoptera	Panorpidae	*Panorpa cognata* L.	87%	W	28	2	9	**17**	27	2	8	**17**									1		1	
		Panorpa alpina Rambur	74%	W	425	64	174	**187**									59	**27**	24	8	366	37	150	**179**
		Panorpa vulgaris Imhoff & Labram	67%	W	5	1	**3**	1					4	1	**2**	1					1		1	
		Panorpa communis L.	61%	–	1904	462	673	**769**	730	240	**279**	211	128	21	**55**	52	511	103	189	**219**	535	98	150	**287**
		Panorpa germanica L.	55%	–	1929	555	**792**	582					136	26	**56**	54	1209	332	**537**	340	584	197	**199**	188
		N individuals			4291	1084	1651	1556	757	242	287	228	268	48	113	107	1779	462	750	567	1487	332	501	654
		N species; with ≥ 5 inds.			5	5	5	5	2	2	2	2	3	3	3	3	3	3	3	3	5	3	5	3
All taxa		N individuals			8285	1842	3380	3063	1770	622	612	536	2344	202	1191	951	2079	516	873	690	2092	502	704	886
		N species; with ≥ 5 inds.			50	44	46	45	28	23	22	23	39	27	32	30	30	20	18	23	28	17	21	21
		N species; incl. «rare» species			79	59	60	58	37	26	25	29	56	35	40	35	36	22	21	25	33	19	24	22

amounts to 100% (see e.g. five top species of Chrysopidae in Table 2). A maximum negative impact is indicated with 0% specimens caught in the disturbed plots ID and HD, as shown in *Sympherobius pellucidus* and *Conwentzia psociformis*. 28 species above 66% are considered to have been winners in the years after the impacts, and 9 are losers in the sense that their abundance was less than 33% in the disturbed areas. 11 species were ranking between 33% and 66%. Two species of both the orders Raphidioptera and Mecoptera, as well as of the neuropteran family Myrmeleontidae, benefited from the disturbances. In the neuropteran family Chrysopidae 10 of 16 species benefited from the disturbances and in the Hemerobiidae 9 of 15 species, whereas in the Coniopterygidae 4 of the 9 species ranked as losers.

Discussion

For most Neuropterida and Mecoptera in Central Europe the basic ecological requirements for larval development and habitat of adults are well known. A majority of species in Switzerland are considered to depend on trees and bushes for development (Aspöck et al. 1980). In particular, the edges of forests are hotspots for neuropteran diversity (Duelli et al. 2002b). In earlier assessments of windthrow effects on Neuropterida after storm Vivian (Duelli et al. 2002b), a significant increase in numbers of species and a highly significant increase in abundances were observed. The same effect was seen after forest fires in Ticino (Moretti et al. 2006). A large majority (74%) of species treated here became more frequent after windthrow and forest fires, basically independent of the type of disturbance. The two forest fire projects show that there is a positive effect on most neuropteran species both when the fire acted during the dormancy period in winter (Forest fire I, Ticino) and during the flight period in summer (Forest fire II, Leuk).

The two windthrow projects show that in both coniferous and deciduous forests and both at higher and lower elevations storms enhanced neuropteran diversity and abundance.

While this might be obvious for species living in open natural or rural landscapes, most of the species found in this study are known to be forest dwellers (Aspöck et al 1980). Why should a forest dweller profit from disturbances destroying the forest? The insects do not profit from the event itself, but from the modified forest structure and abiotic condition, which in turn become similar to the conditions at forest edges (Duelli et al 2002a). In destroyed forests, more sunlight reaches the floor and allows regrowth of herbs, bushes and young trees, which are attractive for plant lice and other soft-bodied arthropods. These in turn are prey to Neuroptera and Raphidioptera, and when injured or dead also for Mecoptera. The sunlight in open gaps favors their reproduction and larval development on herbs and bushes, as well as on the newly created inner forest edges.

Analyzing the neuropteran species composition in different types of forest edges along the vertical vegetation gradient (Duelli et al. 2002a) showed that only 5% of the species living in forest habitats were more abundant within the forest than at the forest edges or in the canopy. In that study, most of the species (29%) reached their maxima in the forest mantle (10–30 m high), 18% in the shrub belt (2–10 m) and 18% in the herbaceous fringe (0–2 m) bordering the forest edges. Three species were only collected in the canopy, whereas seven species were collected in the contact zones between forest and open space from the shrub belt to the canopy. Thus, most of the neuropteran species were in fact forest edge species (Duelli et al. 2002a).

In the four projects presented here, the top winners after fire and windthrow (Table 1) were the species with all specimens collected exclusively in the disturbed plots. The highest number of species (46) was found in the intermediately disturbed (ID) plots, closely followed by the 45 species with maxima in the heavily disturbed (HD) plots. Looking at the different taxonomic groups, however, reveals clear differences.

Neuroptera: Chrysopidae

Among the six top winners with 100% in disturbed plots were five green lacewing species. Two of these, *Chrysopa formosa* and *C. pallens*, are known to live in open habitats, on herbs or bushes (Aspöck et al. 1980). The three others, *Nineta flava, Pseudomallada prasinus* and *P. ventralis,* like almost all other winners among the Chrysopidae, are well-known forest edge species (Duelli et al. 2002a) or ubiquists (exemplified by *Chrysoperla lucasina* or *C. carnea*). *Hypochrysa elegans*, a pollen feeder in the adult stage, requires flowering plants for egg production. The arboreal *Chrysoperla pallida* and *Nothochrysa fulviceps* showed no clear preferences for disturbed habitats. Clear losers among the Chrysopidae were *Peyerimhoffina gracilis*, restricted to shady conifer forests, and *Chrysotropia ciliata*, mainly found in the Windthrow I project Lothar, which is known to live in moist forest habitats.

Neuroptera: Hemerobiidae

It was a surprise to see so many hemerobiid species ranking high up as winners after disturbances, because hemerobiids are known among neuropterologists to live mainly in the forest interior. However, *Wesmaelius malladai, Micromus paganus, Megalomus hirtus* and *M. tortricoides*, as well as the abundant *Wesmaelius subnebulosus,* can also be found in open habitats (Aspöck et al. 1980), and *Micromus variegatus* is even common in crop fields (McEwen et al. 2001). In forest edges, the *Micromus* species were labeled "herbaceous fringe" species (Duelli et al. 2002a), which is the lowest layer between forest edge and open habitat. *Hemerobius lutescens* and *Drepanepteryx phalaenoides* were considered "mantle-species." Among the losers, the genus *Sympherobius*, represented by three small species, was dominant. A clear loser also was *Hemerobius pini*, again a specialist on conifers (Aspöck et al. 1980). More than half of the species of Hemerobiidae were not abundant enough to be treated here (see Appendix 1).

Neuroptera: Coniopterygidae

These tiny insects fly only within a small range when disturbed, but sometimes can swarm and move to other habitats in the morning. *Parasemidalis fuscipennis*, *Coniopteryx esbenpeterseni, C. borealis,* and *C. tineiformis* were found mostly in disturbed plots. The rather rare *C. haematica and C. drammonti* (both only Ticino), as well as the abundant *Semidalis aleyrodiformis*, showed no clear preferences for disturbed habitats. Losers were *C. pygmaea*, and especially *Conwentzia psociformis.*

Neuroptera: Myrmeleontidae

Only two species of antlions were collected in sufficient numbers to be treated here, and both were favored by the effects of fire. *Distoleon tetragrammicus*, recorded only in the forest fire project II above Leuk, clearly favored ID plots. The species is known to develop in detritus between tree roots in warm forests (Aspöck et al. 1980). *Myrmeleon formicarius*, the most common antlion in Switzerland, was also collected only at Leuk, with nine specimens in the ID plots and three in the FO plots.

Raphidioptera

The two most abundant snake fly species were winners. The most positive impact of disturbance was shown in *Phaeostigma notata*, a "mantle species" in forest edges (Duelli et al 2002a). The larvae live under bark, where they feed on other arthropods, such as the larvae of bark beetles (Kenis et al. 2004). The larvae are most frequent under loose bark of dead tree trunks, thus favored by both types of disturbance. In the Lothar windthrow II and Leuk forest fire II projects they were most abundant in ID plots, and in the Vivian windthrow I they were most abundant in the cleared (HD) plot. *Dichrostigma flavipes* was caught only in the Leuk project, but in large numbers, mainly in the ID plots. The species develops in the soil in coniferous as well as deciduous forests (Aspöck et al. 1980). *Puncha ratzeburgi*, also a "mantle species" in forest edges (Duelli et al. 2002a), develops under bark of conifers and was collected in all three disturbance conditions of the Vivian and Leuk projects.

Mecoptera

All four *Panorpa* species had more specimens in the disturbed plots, but only two were winners with more than 66%. *Panorpa cognata*, almost exclusively found in the Forest fire I project in Ticino, was about equally frequent in ID (24) and HD (22) plots, with only 2 specimens collected in the intact forest. Like all *Panorpa* species, *P. cognata* develops in the soil (Willmann 1989). *Panorpa alpina* was collected in surprisingly large numbers in the Lothar (Windthrow II) project, far from "alpine" regions. While most frequent in ID and HD plots in the Windthrow II project, the species was most frequent in the intact forest (FO) in the Windthrow I project. *Panorpa communis*, the most abundant species in this study, preferred ID plots after fire, whereas the numbers in the windthrow projects were highest in the HD plots. *Panorpa germanica*, not recorded in Ticino, benefitted least in overall numbers from the disturbances among the Mecoptera, but was consistently most abundant in the ID plots.

Conclusion

The combined results of our four independent projects suggest that strong natural disturbances such as windthrow or wildfire, which humans consider to be catastrophes, but which have proven to enhance biodiversity in various taxa, are positive also for most Neuroptera, Raphidioptera, and Mecoptera by increasing their abundance in the years after fires and windthrows.

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Appendix 1

Species collected with less than 5 specimens. The Hemerobiidae dominated, whereas no rare Mecoptera were collected. Most scarcely collected species were caught in the forest fire II plots above Leuk, followed by the forest fire I plots in Ticino.

Order	**Family**	**Species**	**Total**	**Forest Fire I**	**Forest Fire II**	**Windthrow I**	**Windthrow II**
Neuroptera	Chrysopidae	*Chrysopa viridana* Schneider	1		1		
		Chrysoperla mediterranea (Hölzel)	1		1		
		Nineta inpunctata (Reuter)	1			1	
		Nineta pallida (Schneider)	4		3	1	
		Nineta vittata (Wesmael)	3			2	1
	Hemerobiidae	*Drepanepteryx algida* (Erichson)	1		1		
		Hemerobius contumax Tjeder	2	1	1		
		Hemerobius fenestratus Tjeder	2			1	1
		Hemerobius gilvus Stein	3	3			
		Hemerobius marginatus Stephens	3	2			1
		Hemerobius nitidulus Fabricius	2		2		
		Hemerobius stigma Stephens	4	1	3		
		Micromus lanosus (Zeleny)	1		1		
		Psectra diptera (Burmeister)	1			1	
		Sympherobius pygmaeus (Rambur)	1		1		
		Wesmaelius balticus (Tjeder)	1		1		
		Wesmaelius concinnus (Stephens)	2		2		
		Wesmaelius fassnidgei (Killington)	3		3		
		Wesmaelius mortoni (McLachlan)	1		1		
		Wesmaelius nervosus (Fabricius)	3	3			
		Wesmaelius quadrifasciatus (Reuter)	4		4		
	Conioptery-gidae	*Coniopteryx arcuata* Kis	1	1			
		Coniopteryx lentiae Aspöck & Aspöck	2	2			
		Conwentzia pineticola Enderlein	2		1	1	
		Helicoconis pseudolutea Ohm	1	1			
	Myrmeleontidae	*Euroleon nostras* (Fourcroy)	2		2		
	Osmylidae	*Osmylus fulvicephalus* (Scopoli)	2				2
Raphidioptera	Inocelliidae	*Parainocellia bicolor* Costa	3	3			
	Raphidiidae	*Xanthostigma xanthostigma* Schummel	3		1		2